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A CYTOTAXONOMIC STUDY OF A NATURAL HYBRID BETWEEN AGROPYRON CRISTATUM AND A. SUBSECUNDUM

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Reports of interspecific hybrids in the Tribe Triticeae of the Gramineae have become commonplace except for those involving diploid *A. cristatum* (L). Gaertn. Grass hybrids involving New World and Old World *Agropyron* are few in number (Dewey, 1967; 1964a; 1964b; (1961). The present paper reports an *A. cristatum* hybrid found by the authors near the United States Forest Service boundary above Mendon, Utah in 1962. Two species of *Agropyron* were closely associated with the hybrid: *A. cristatum* and *A. subsecundum* (Link) Hitchc. Bowden (1965) and some other investigators have accepted the combination *A. trachycaulum* (Link) Malte for this entity and regard *A. subsecundum* as an awned variety of *A. trachycaulum*. No other species of *Agropyron* was found in the area after a careful search. *Elymus glaucus* Buckl. and *Hordeum jubatum* L. were present in the area but not in abundance and not near the hybrid. Specimens of the species and hybrid discussed in this paper are deposited at the Intermountain Herbarium at Utah State University.

Comparative Morphology of Putative Parents and Hybrid. The diploid *A. cristatum* growing within inches of the hybrid had glumes distorted near the base, curved awns, and blades strongly pilose on the ventral surface. These morpholological characters will usually separate the diploid *A. cristatum* from the tetraploid, *A. desertorum,* where the glumes and awns are straight and the ventral surface of the blades glabrous or only slightly pilose. *Agropyron subsecundum* was typical of the plants found in northern Utah. The single bunch of the hybrid was conspicuous, as it appeared to be intermediate in most characters between the suspected parents.

The hybrid plant as it was found on the mountain produced spikes with solitary spikelets at each node of the rachis but clonal material grown in the field nursery had a tendency to produce two spikelets at a node on the lower part of the spike. *Agropyron subsecundum* and *A. trachycaulum* often do this when grown under optimal ecological conditions. *Agropyron cristatum* produces a single spikelet at each node under all conditions.

The spikelets of the sterile hybrid were not as crowded and strongly divergent as those of diploid *A. cristatum* but not as distant and appressed to the rachis as those of *A. subsecundum*. In these characters and the length of the spike the hybrid was intermediate between the putative parents (fig. 1). The glumes of the hybrid were only slightly distorted at the base and the awns were nearly straight, and the leaf blades were only slightly pilose on the ventral surface.

Cytological Studies. Both presumed parents had normal meiotic divisions. *Agropyron cristatum*, 2n = 14, regularly formed 7_{II} at metaphase I, in general confirming the observations of Dewey (1964a). *A. subsecundum*, 2n = 28, is an allotetraploid regularly forming 14_{II} at metaphase I and the meiotic behavior did not depart significantly from that described by Dewey (1966).

Tbe sporophytic chromosome number of the hybrid is 21, as expected in view of the virtually certain progenitors described above.

It is questionable whether any gene exchange occurs between chromosomes in the hybrid. Of the 185 plates interpreted at diakinesis and metaphase I, 39 percent had 21 perfectly clear univalents (fig. 1). The remainder possessed a puzzling kind of chromosomal association involving one or two "pairs" of chromosomes. In 23 percent of the plates there were 19 univalents plus two chromosomes connected terminally by a slender matrix-like thread. In 14 percent there were 17 univalents and two "matrix pairs" present. In 11 percent there were one or two "pairs" of chromosomes associated simply end-to-end with no indication of an unterminalized region that is generally characteristic of rod bivalents in the Triticeae. The possibility of relatively rare formation of a chiasma in one arm cannot, however, be dismissed. The association observed may be of a homoeologous nature.

At telophase I, The univalents were distributed approximately equally to the poles. Frequently the chromatids were not well defined in contrast to normal telophase dyads. Equational division of univalents was rare. Lagging chromosomes were frequent but less numerous than in many hybrids in this tribe. Characteristically, telophase I chromosomes in the Triticeae do not return to the interphasic condition; only a partial relaxation of the coils occurs prior to re-orientation on the metaphase II plate. Telophase I chromosomes in the present hybrid were an exception to this. Increase in length and decrease in stainability was pronounced.

In most grass hybrids the lagging univalents that fail to become included within the nucleus at telophase I become spherical, very darkly staining micronuclei in the cytoplasm. This occurs to a limited extent in the present hybrid but in addition there exists another and more striking kind of micronuclei: one or many lagging chromosomes remain outside the nucleus, uncoil, and apparently become surrounded by a membrane. In addition, partially uncoiled chromosomes may be present outside the nucleus not surrounded by a membrane.

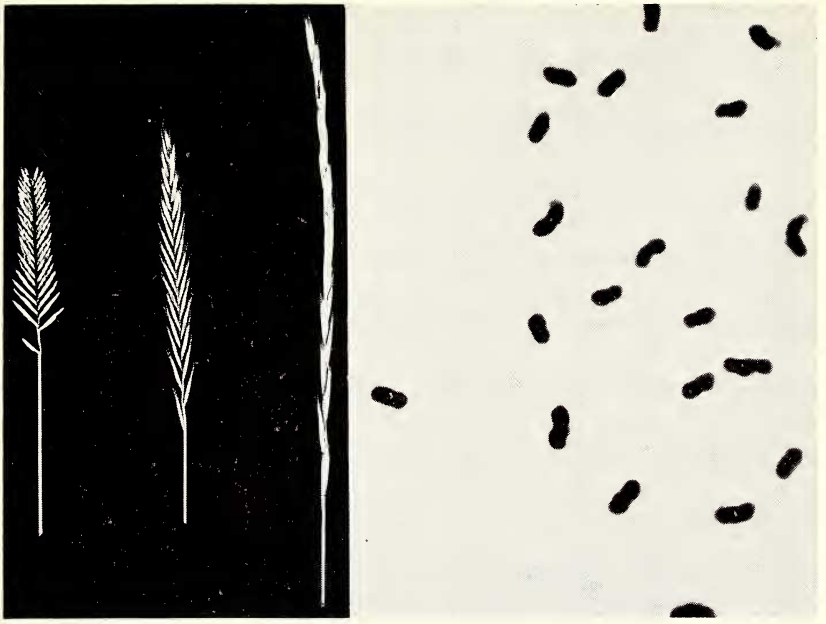

FIG. 1. Spikes of *Agropyron cristatum* (left), *A. subsecundum* (right), and the hybrid × 2/3. Metaphase I in the hybrid, PMC. 21_I, × 2400.

In the second division the chromosomes divided equationally in an essentially normal fashion and were distributed in approximately equal numbers to the poles. Laggards were often present and these formed typical micronuclei at the conclusion of the division. The unusual type of micronuclei described above for telophase I were not generally found at telophase II.

A substantial portion of the pollen mother cells never completed meiosis. Most mature anthers contained approximately half the normal number of pollen grains; some were virtually empty.

Many thousands of pollen grains have been observed in control plants during the course of radiobiological studies on this hybrid. All were judged to be sterile on the basis of staining reaction and abnormal, deformed structure. The hybrid is completely sterile.

Root tip squash preparations disclosed 21 chromosomes. The divisions were entirely normal and the plants of hybrid clones were unusually vigorous and hardy.

Braegger (1966), in a karyotype analysis of this hybrid, reported chromosome lengths ranging from 6.5–11.5 u in a closely graduated series. All chromosomes possess median or sub-median centromeres. Bottino (1965) reported cyto-genetic effects of gamma irradiation on this hybrid.

Hybridization Attempts. Extensive attempts to produce a controlled *A. cristatum—A. subsecundum* hybrid were made in 1965 and 1966. Two special difficulties attend crossing these species: *A. subsecundum* flowers in early June and the florets open in the morning hours. *A. cristatum* flowers in late June and the florets open in the afternoon. The overlap time is short indeed.

In view of the reported self sterility of *A. cristatum* (Dewey, 1963) synthesis of the hybrid was attempted the first year without emasculation, with this species serving as the female parent. Both hand pollination, and pollinator culms of *A. subsecundum* sustained in bottles of water were utilized. The spikes were subsequently bagged. In all, 412 spikes of *A. cristatum* were used, and 212 seeds later obtained. Of these, 125 germinated and produced seedlings all of which proved to be selfed *A. cristatum*. Obviously, under the conditions of this experiment, some strains of *A. cristatum* are not self sterile.

In the second year approximately 20 florets in each of 95 spikes of *A. subsecundum* were emasculated and utilized as female parents. Thirty-three of the emasculated spikes were hand pollinated with pollen obtained from early maturing plants of *A. cristatum* grown in the greenhouse, and bagged. The remainder were bagged with pollinater culms of *A. cristatum* sustained in bottles of water in the conventional fashion. Ninety-five seeds were obtained, 51 of which germinated to produce vigorous seedlings. Root tip squash preparations disclosed that all 51 possessed 28 chromocomes and were not hybrids. It is difficult to see how such a high percentage of selfed *A. subsecundum* seeds could be obtained with the precautions taken. The possibility of apomictic development is therefore being investigated.

Diploid agropyrons in the Intermountain region are known only in the native *A. spicatum* and the introduced *A. cristatum*. This gives strong support that *A. cristatum* must be one of the parents of the triploid hybrid. Spike length, straight awns and proximity of the *A. subsecundum* to the hybrid suggests that this is in all probability the second parent.

We were unable to distinguish, with confidence, between chromosomes of *A. cristatum* and *A. subsecundum* in pollen mother cell divisions of the hybrid (fig. 1). Braegger (1967) was also unable to do this with mitotic chromosomes in root tip studies. However, he did find that the largest, satellited, and readily identifiable chromosome in the hybrid had a precise counterpart in *A. subsecundum*. In addition his total chromosome length studies in the hybrid and the presumed parents are closely consistent with the suggested origin of the hybrid.

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THE WATER HYACINTH IN CALIFORNIA

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Eichhornia crassipes (Mart.) Solms. (Pontederiaceae) commonly is called water hyacinth. The first record of *E. crassipes* in California was from a slough near Clarksburg, Yolo Co. (*Smith,* Sept. 30, 1904, UC). The first published account (Johnson, 1920) recorded it from the Centerville Bottoms, King River System, Fresno Co. I have found *E. crassipes* to be naturalized in California in the Kings, Tuolumne, San Joaquin, and Sacramento rivers systems (fig. 1). The northern limit of naturalization for this species in California was found in Babel Slough, about 10 miles northwest of Sacramento. This may be a world-wide northern limit for the weedy distribution of this species. The southern limit in California was in a pond draining from Lake Hodges, Clevenger Canyon, Ramona, San Diego Co. (*Franklin & Buckner,* Nov. 29, 1967, SD). The distribution of water hyacinths in California appears to be expanding since its early sightings in Yolo and Fresno counties. It still is found in these locations as well as in several new places (fig. 1). The distribution map is based upon personal observation and upon herbarium specimens (CAS, DAV, DS, Fresno State College, GH, LA, ND, NY, POM, RSA, SD, UC, UCR, UCSB, and US).

Unfortunately, no record exists of the progressive spread of *E. crassipes* in California, so that we must surmise how it occurred. Almost certainly, the species was introduced into the state by man as an ornamental. Subsequently, plants were put into California waterways. Plants from the Kings River system could have spread to the San Joaquin because of their proximity north of Fresno. And it is not difficult to imagine plants moving